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Differences in Shade Tolerance Help Explain Varying Success of Two Sympatric Alnus Species

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Abstract
Alnus maritima and *Alnus serrulata* are riparian shrubs that occur in similar habitats in the southern and eastern United States.*Alnus serrulata* is abundant throughout this range, but *A. maritima* is rare, occurring only in small populations in Oklahoma and Georgia and on the Delmarva Peninsula. *Alnus maritima* is more resistant than *A. serrulata* to water and temperature stresses, but the degree to which insolation influences the restricted distribution of *A. maritima* is unknown. Our goals were to characterize the shade tolerance of *A. maritima* and *A. serrulata* and determine whether differences in shade tolerance could help explain the differing ecological success of the two species. Measurements in nature showed that leaves of *A. serrulata*have greater concentrations of chlorophyll than do leaves of *A. maritima*, and a greater percentage of *A. serrulata* inhabit shaded sites. Two experiments evaluating the resistance of seedlings to light-deficit stress revealed that *A. maritima* had a greater photosynthetic capacity and grew more quickly than *A. serrulata* in full sunlight. In shade, survival of seedlings was lower and reductions in photosynthesis and growth were greater for *A. maritima* than for *A. serrulata*. We conclude that *A. serrulata* is tolerant and *A. maritima* is intolerant of shade. Moreover, we conclude that shade intolerance strongly restricts the potential niches of *A. maritima* within the region where the shade-tolerant *A. serrulata* is comparatively abundant.

Keywords
Alnus maritima, Alnus serrulata, light requirements, photosynthetic response, realized niche

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DIFFERENCES IN SHADE TOLERANCE HELP EXPLAIN VARYING SUCCESS OF TWO SYMPATRIC *ALNUS* SPECIES

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Alnus maritima and *Alnus serrulata* are riparian shrubs that occur in similar habitats in the southern and eastern United States. *Alnus serrulata* is abundant throughout this range, but *A. maritima* is rare, occurring only in small populations in Oklahoma and Georgia and on the Delmarva Peninsula. *Alnus maritima* is more resistant than *A. serrulata* to water and temperature stresses, but the degree to which insolation influences the restricted distribution of *A. maritima* is unknown. Our goals were to characterize the shade tolerance of *A. maritima* and *A. serrulata* and determine whether differences in shade tolerance could help explain the differing ecological success of the two species. Measurements in nature showed that leaves of *A. serrulata* have greater concentrations of chlorophyll than do leaves of *A. maritima*, and a greater percentage of *A. serrulata* inhabit shaded sites. Two experiments evaluating the resistance of seedlings to light-deficit stress revealed that *A. maritima* had a greater photosynthetic capacity and grew more quickly than *A. serrulata* in full sunlight. In shade, survival of seedlings was lower and reductions in photosynthesis and growth were greater for *A. maritima* than for *A. serrulata*. We conclude that *A. serrulata* is tolerant and *A. maritima* is intolerant of shade. Moreover, we conclude that shade intolerance strongly restricts the potential niches of *A. maritima* within the region where the shade-tolerant *A. serrulata* is comparatively abundant.

Keywords: *Alnus maritima*, *Alnus serrulata*, light requirements, photosynthetic response, realized niche.

Introduction

Alnus serrulata (Ait.) Willd. is among the most abundant of North American *Alnus* species and is found in most of the southern and eastern United States. In contrast, *Alnus maritima* (Marsh.) Muhl. ex Nutt. is rare; it occurs as three widely disjunct subspecies in Oklahoma (subsp. *oklahomensis* Schrader & Graves), Georgia (subsp. *georgiensis* Schrader & Graves), and Delaware and Maryland on the Delmarva Peninsula (subsp. *maritima*); it is sympatric with *A. serrulata* in two of these locations (fig. 1). For years, botanists had speculated about the origin of the peculiar distribution of *A. maritima*. Most believed that *A. maritima* evolved on the Delmarva Peninsula and that this population (subsp. *maritima*) was the progenitor of the other two subspecies. Some also believed that the Georgia and Oklahoma populations were the result of long-distance dispersal by Native Americans (Stibolt 1981). More recently, it was demonstrated that the subspecies of *A. maritima* are remnants of a continuous distribution comparable to that of *A. serrulata* (Furlow 1979; Schrader and Graves 2002, 2004). Furlow (1979) proposed that the present disjunct distribution of *A. maritima* originated by isolation of the populations after range restriction but did not identify causal factors. Explanations to date for the rarity of *A. maritima* and the apparent ecological superiority of *A. serrulata* are incomplete. *Alnus maritima* expresses greater seed germinability, greater resistance to water and temperature stresses, and a greater rate of growth than does *A. serrulata* (Shopmeyer 1974; Hennessey et al. 1985; Schrader and Graves 2000, 2003; Schrader et al. 2005). With all the available evidence indicating that *A. maritima* has a broader fundamental niche (range of resources usable by an organism in the absence of interspecific competition; Hutchinson 1978) than *A. serrulata*, we examined whether shade tolerance, an important component of interspecific competition, might be a factor in the varying success of the two species.

Most species of *Alnus* are considered shade intolerant (Furlow 1979), and preliminary observations suggest that *A. maritima* is no exception. Germinated seeds of *A. maritima* establish well under moderate or high light (PAR $\geq$ 400 μmol m^{-2} s^{-1}), but under conditions of low light (PAR $\leq$ 150 μmol m^{-2} s^{-1}), growth is severely retarded, and seedlings eventually die (Schrader 1999). Demographics of the three natural populations also suggest shade intolerance (Schrader and Graves 2002), but direct comparisons of the shade tolerance of *A. maritima* and *A. serrulata* have not been made. Our goals were to classify and characterize the shade tolerance of *A. maritima* and *A. serrulata*, to determine the extent to which shade intolerance limits the potential niches of *A. maritima*, and to determine whether differences in the shade tolerance of the two species could help explain why *A. maritima* occupies a small and patchy distribution within a large region in which *A. serrulata* is distributed broadly.

As an initial step in evaluating the shade tolerance ecology of the two species, we characterized the cover density, leaf chlorophyll content, chlorophyll *a* : *b* ratio, and specific leaf mass of plants growing in natural populations. We also

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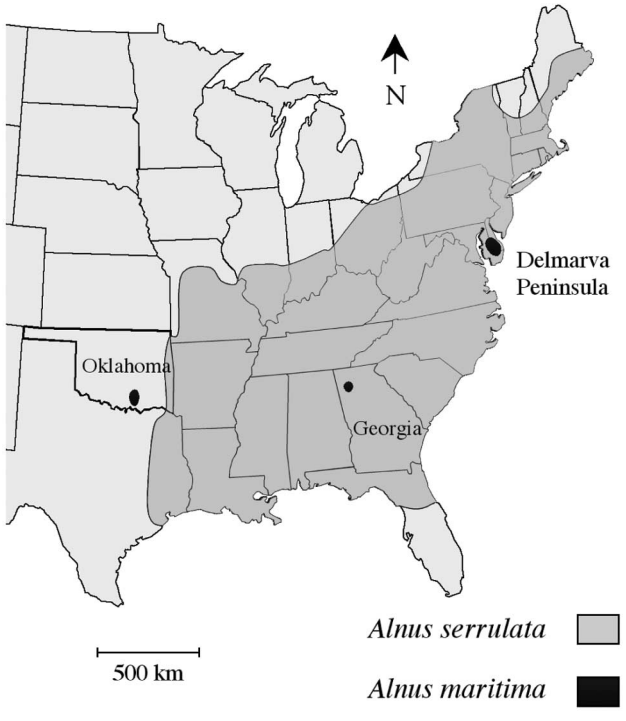

Fig. 1 Geographical distribution of *Alnus maritima* and *Alnus serrulata*. *Alnus serrulata* is abundant throughout the eastern United States, while *A. maritima* is rare and grows sympatrically with *A. serrulata* in Georgia and on the Delmarva Peninsula in Delaware and Maryland.

examined the shade tolerance of the species in two experiments, first by measuring the survival and growth of young seedlings under full ambient PAR plus 16 h of artificial PAR and under 80% and 98% reductions in PAR in a greenhouse for 5 wk. Second, we measured leaf chlorophyll, photosynthesis, growth, and dry-mass partitioning of older seedlings under full ambient sunlight or shade (96% reduction) in the landscape for 4 mo. Our results provide new insights concerning the ecology, ecophysiology, and shade tolerance of *A. maritima* and *A. serrulata*.

Material and Methods

Plants in Natural Populations

In May 2004, naturally occurring *Alnus maritima* and *Alnus serrulata* in the three disjunct areas where *A. maritima* is found were examined for cover density, leaf chlorophyll content, chlorophyll *a* : *b* ratio, and specific leaf mass. Each individual plant (a distinct clump of branches emerging from the ground) was considered an observational unit. On the Delmarva Peninsula, observational units of *A. serrulata* and *A. maritima* subsp. *maritima* were sampled at a swamp near Sharpstown, Maryland (38°32.899′N, 75°43.369′W); along the Nanticoke River near Eldorado, Maryland (38°34.661′N, 75°47.553′W); along Marshyhope Creek near Hurlock, Maryland (38°37.848′N, 75°49.106′W); and on the banks of Hudson Pond north of Georgetown, Delaware (38°50.295′N, 75°26.362′W). *Acer rubrum* L., *Nyssa sylvatica* Marsh., and *Quercus macrocarpa* Michx. were prominent members of the overstory that shaded some of the *Alnus* at these locations. In Georgia, plants of the two species were examined in Drummond Swamp near Euharlee (34°07.837′N, 84°57.025′W), the location of the only natural population of *A. maritima* subsp. *georgiensis* that is known. Overstory trees (mostly *A. rubrum*, *Acer negundo* L., *Quercus nigra* L., and *Platanus occidentalis* L.) shaded some of these plants. Because *A. serrulata* and *A. maritima* are not sympatric in Oklahoma, the two species were sampled from their closest populations (ca. 95 km apart, east to west). Individuals of *A. serrulata* were examined along three small creeks in the Hamden Unit of the Hugo Wildlife Management Area east of Antlers (from 34°08.529′N, 95°33.138′W to 34°08.534′N, 95°32.262′W). *Betula nigra* L., *P. occidentalis*, and *Ulmus americana* L. were the predominant overstory species that shaded some of these individuals. Plants of *A. maritima* subsp. *oklahomensis* were sampled on the banks of the Blue River in the Blue River Wildlife Management Area north of Tishomingo (34°21.538′N, 96°35.743′W). Overstory trees (mostly *Q. macrocarpa*, *P. occidentalis*, and *Juglans nigra* L.) shaded some of these plants. Accessible plants of the two species were examined and sampled at each geographic site. Preliminary analyses indicated no significant effects for sites within populations, so results for separate sites were nested within populations. The number of *A. maritima* sampled was 30, 30, and 20 for the Delmarva, Georgia, and Oklahoma populations, respectively. The number of *A. serrulata* sampled was 30, 10, and 20 for the Delmarva, Georgia, and Oklahoma populations, respectively.

Shading on the north, east, south, and west sides of each plant was measured using a handheld spherical densiometer (Lemmon 1956; Englund et al. 2000). These measurements were converted and averaged to quantify the percentage of open sky above each plant. An exposed leaf was selected randomly from each plant and analyzed for chlorophyll content and specific leaf mass. A 38.5-mm^2 disk was removed with a cork borer from the left-apical quarter of each leaf blade. Each disk was placed in a closed test tube for chlorophyll extraction with 3 mL *N*,*N*-dimethylforamide (DMF) (Moran and Porath 1980; Inskeep and Bloom 1985). Chlorophyll was extracted over 24–48 h in a dark, ice-filled cooler during transport to the laboratory. Absorbances at 647 and 664.5 nm were measured by dual-beam spectrophotometry by using a DMF blank. Chlorophyll *a* and *b* concentrations in the extract were calculated from the formulas of Moran and Porath (1980) and Inskeep and Bloom (1985). The remainder of each leaf was dried in an oven and weighed. Area was determined by tracing on graph paper. Correction was made for the area and mass of the disk that had been removed for chlorophyll analysis. Chlorophyll content per gram was calculated using specific leaf mass for each leaf. For analysis of chlorophyll and specific mass, observational units were placed into "high-light" ($\geq$50%) and "low-light" ($<$50%) subcategories based on the percentage of open sky above each unit. Subcategorical replication for *A. maritima* was $N = 15$, 19, and 10 for plants growing under high light in Delmarva, Georgia, and Oklahoma, respectively, and $N = 15$, 11, and 10 for plants growing under low light in

Delmarva, Georgia, and Oklahoma, respectively. Subcategorical replication for *A. serrulata* was $N = 11$, 5, and 10 for plants growing under high light in Delmarva, Georgia, and Oklahoma, respectively, and $N = 19$, 5, and 10 for plants growing under low light in Delmarva, Georgia, and Oklahoma, respectively.

Tolerance of Young Seedlings to Shade Stress

Seeds of *A. serrulata* and *A. maritima* subsp. *oklahomensis* were collected from naturally occurring plants near Cass, Arkansas (35°41′47.65″N, 93°49′37.32″W), and Tishomingo, Oklahoma (34°19′16.92″N, 96°35′44.16″W), respectively. On February 8, 2005, seeds were placed in moist stratification at 4°C for 3 wk and then held for 10 d in germination conditions (24°C in the dark), as described by Schrader and Graves (2000). On March 11, 2005, seedlings were placed singly in peat-based soilless root medium in separate plastic pots (8cm × 8 cm square × 10 cm deep), randomized among three PAR treatments ($N = 30$ for each species in each treatment), and held on a greenhouse bench for 5 wk. The control treatment consisted of full ambient PAR plus 16 h of artificial PAR from 0600 to 2200 hours each day. Moderate-shade and deep-shade treatments were held on the same bench, but plants were covered by shade fabric (80% reduction) or full-opacity polyethylene tarp (98% reduction), respectively. Mean PAR levels between 1000 and 1400 hours for the full-PAR, moderate-shade, and deep-shade treatments were 473, 95, and 9 μmol m^{-2} s^{-1}, respectively, and mean greenhouse temperature and relative humidity were 23.4°C and 39.7%. The root medium for each unit was kept moist over the duration of the experiment by subirrigation (the bottom 1 cm of each pot was immersed continuously in tap water). Seedlings were harvested on April 14, 2005, and measured for percentage survival, shoot height, leaf count (number of leaves $\geq$3 mm long), plant mass after drying at 60°C for 3 d, and leaf mass ratio (ratio of leaf dry mass to whole-plant dry mass).

Effects of Shade Stress on Photosynthesis, Growth, and Carbon Allocation

Seeds of naturally occurring *A. maritima* and *A. serrulata* were collected and stratified for 3 wk (Schrader and Graves 2000). Seeds of *Cercis canadensis* L. (shade-tolerant control) and *Robinia pseudoacacia* L. (shade-intolerant control) were collected near Ames, Iowa, and were scarified according to the methods of Shopmeyer (1974). Seeds of all four species were placed into germination conditions (24°C in the dark) on February 14, 2003, and held for 10 d. Seedlings were placed singly in peat-based soilless root medium in separate plastic pots (top diameter = 15.2 cm, height = 15 cm), and the pots were placed randomly on a greenhouse bench under either full ambient PAR or shade fabric (80% reduction), according to the treatment they would receive in a field plot. On May 23, 2003, 240 3-mo-old seedlings (120 *A. maritima* [40 each from the three subspecies] and 40 each of the other three species) were randomized and installed 2 m apart in a field plot at a research station of Iowa State University in Ames. According to their randomized treatment assignments, plants either received full ambient sunlight or were covered by an individual full-opacity shade covering (a wire cage with top covered by black polypropylene tarp, 96% reduction) for 4 mo. Individual coverings were 66 cm in diameter × 76 cm tall for the smaller plants (*Alnus*) and 92 cm in diameter × 116 cm tall for the larger plants (*C. canadensis* and *R. pseudoacacia*). Plants were irrigated twice weekly and received supplemental liquid fertilizer (Peters Excel All-Purpose and Cal-Mag; 16.5N-2.2P-13.5K; Grace-Sierra Horticultural Products, Milpitas, CA; 11.0 mM) once each month. Mean PAR levels between 1000 and 1400 hours were 1557 and 64 μmol m^{-2} s^{-1} for sun and shade treatments, respectively, during the 4-mo experiment (table 1).

On August 6, 2003, net photosynthetic rates at mean midday treatment PAR levels (mean PAR between 1000 and 1400 hours, 1575 and 65 μmol m^{-2} s^{-1} for sun and shade treatments, respectively, as of August 6) were measured with a LI-COR 6400 Portable Photosynthesis System (LI-COR, Lincoln, NE) on the youngest fully expanded leaves of 30 and 10 randomly selected plants per treatment for *A. maritima* (10 of each subspecies) and each of the other three species, respectively. After each gas exchange measurement, disks were collected from each assayed leaf and analyzed for chlorophyll content, chlorophyll *a* : *b* ratio, and specific leaf mass by using the same methods we used to assess plants in natural populations. Photosynthesis per gram of chlorophyll and photosynthesis per gram of leaf were calculated. On August 8, 2003, photosynthetic light response curves were developed for 12 and four randomly selected plants per treatment for *A. maritima* (four of each subspecies) and each of the other three species, respectively. These data were used to calculate dark respiration (CO_2 evolved at 0 PAR), PAR compensation point (PAR level at which the photosynthesis rate matched the rate of respiration), and photosynthetic efficiency (Loach 1967; increase in photosynthesis per unit PAR from 0 to 400 μmol m^{-2} s^{-1}, calculated as the slope of the linear regression for photosynthesis at PAR of 0, 200, and 400 μmol m^{-2} s^{-1}). All photosynthesis data were obtained between 1000 and 1400 hours.

On September 19, 2003, all plants were measured for shoot height from the soil surface to the tip of the apex and

Table 1

Environmental Conditions during Our Experiment Evaluating the Effects of Shade Stress on Photosynthesis, Growth, and Carbon Allocation of *Alnus maritima* and *Alnus serrulata*

	PAR[a] (μmol m^{-2} s^{-1})			
	Sun treatment	Shade treatment	Temperature[b] (°C)	RH[c] (%)
June	1635	73	22.7	48
July	1514	61	23.3	57
August	1583	64	25.2	50
September	1497	59	18.4	45
Overall mean	1557	64	22.4	50

Note. Conditions were recorded continuously with a datalogger (CR23X, Campbell Scientific, Logan, UT).

[a] Mean PAR between 1000 and 1400 hours.

[b] Mean temperature between 1000 and 1400 hours.

[c] Mean relative humidity between 1000 and 1400 hours.

canopy diameter in the north-south and east-west directions at the height where the canopy was widest. The entire shoot of each plant was then harvested by severing the plant at ground level. Leaf blades ≥1 cm in length were counted, cut from the shoots, and measured for area by using a Model 3100 leaf area meter (LI-COR). Leaf and stem dry masses (tissue mass after drying at 60°C for 3 d) were measured. These data were used to calculate canopy shape (shoot height/canopy diameter), shoot dry mass, leaf : shoot dry-mass ratio, and leaf area density (plant leaf area/canopy volume). Canopy volume was calculated from the three-dimensional shoot measurements.

Statistical Analysis

Data for all experiments were analyzed for main effects, interactions, and means separation statistics by using the general linear models (GLM) procedure and the least significant difference (LSD) option of SAS/STAT, version 6.12 (SAS Institute 1996). Data sets were tested for homogeneity of variance by using Levene's test (SAS Institute 1989), and nonhomogeneous data were transformed by a log or square root function. Means were calculated from raw data, and the means separation statistics were calculated from raw or transformed data as necessary. Graphing and regression procedures of Microsoft Excel 98 (Microsoft 1998) were used to plot light response curves and to calculate PAR compensation points and photosynthetic efficiencies. Our experiment with 3-mo-old seedlings included full replication of the three subspecies of *A. maritima*, but no statistical differences were found among the subspecies for any of the variables; therefore, results for the subspecies were combined to represent the species as a whole.

Results

Plants in Natural Populations

Alnus serrulata was found growing in shadier locations (lower percentage of open sky) in Oklahoma and on the Delmarva Peninsula than was *Alnus maritima* (table 2). Plants in Georgia showed the same trend, but perhaps due to low replication for *A. serrulata* ($N = 10$), the difference between the species was not significant at $P \leq 0.05$. In high light (≥50% open sky), leaf chlorophyll content was different between the two species only in Oklahoma, where leaves of *A. serrulata* contained more chlorophyll than those of *A. maritima*. In low light (<50% open sky), leaves of *A. serrulata* contained more chlorophyll than *A. maritima* leaves in all three provenances (table 2). Leaves of *A. serrulata* from Georgia and Oklahoma had more chlorophyll in low light than in high light, while this plasticity was seen for *A. maritima* only in Oklahoma. The chlorophyll $a : b$ ratio was lower in the leaves of *A. serrulata* than in those of *A. maritima* at both light levels and in all three provenances, except that there was no difference for plants growing in high light in Georgia. There was no difference in chlorophyll $a : b$ ratio of each species in high light and low light. The specific leaf mass of the two species was not different for plants in high light but was greater for plants of *A. maritima* growing in low light (table 2). Plasticity in specific leaf mass (lower specific leaf mass in lower light) was evident for both species but only for plants of the Oklahoma provenance.

Tolerance of Young Seedlings to Shade Stress

Survival of seedlings of *A. maritima* and *A. serrulata* did not differ in full PAR, but seedlings of *A. serrulata* showed

Table 2

Open Sky Percentage, Chlorophyll Characteristics, and Specific Leaf Mass of *Alnus maritima* and *Alnus serrulata* Growing in Natural Habitats on the Delmarva Peninsula, in Northwestern Georgia, and in Southern Oklahoma

	Provenance					
	Delmarva		Georgia		Oklahoma	
Dependent variable	*A. maritima*	*A. serrulata*	*A. maritima*	*A. serrulata*	*A. maritima*	*A. serrulata*
Open sky[a] (%)	52^{A}	22^{B}	$83^{A(A)}$	$62^{A(B)}$	71^{A}	52^{B}
Chlorophyll[b] ($\mu g\ g^{-1}$):						
High light[c]	58^{AB}	62^{A}	42^{B}	40^{B}	44^{C}	58^{B}
Low light	54^{B}	66^{A}	46^{B}	57^{A}	64^{B}	96^{A}
Chlorophyll $a : b$ ratio:						
High light	3.2^{AB}	2.7^{C}	$3.3^{A(AB)}$	$3.3^{A(AB)}$	3.1^{A}	2.6^{B}
Low light	3.4^{A}	3.0^{BC}	$3.5^{A(A)}$	$3.2^{A(B)}$	2.9^{A}	2.4^{B}
Specific leaf mass ($mg\ cm^{-2}$):						
High light	8.4^{A}	7.5^{AB}	$10.1^{A(A)}$	$9.7^{A(AB)}$	11.4^{A}	11.0^{A}
Low light	8.9^{A}	7.1^{B}	$9.9^{A(A)}$	$8.9^{A(B)}$	7.2^{B}	5.12^{C}

Note. Means within a provenance marked by the same letter are not significantly different at $P \leq 0.05$, according to Fisher's least significant difference test (i.e., means separations are full factorial analyses, but each provenance was analyzed separately). Letters in parentheses reflect differences significant at $P \leq 0.10$. $N = 15$, 19, and 10 for plants of *A. maritima* growing under high light in Delmarva, Georgia, and Oklahoma, respectively. $N = 15$, 11, and 10 for plants of *A. maritima* growing under low light in Delmarva, Georgia, and Oklahoma, respectively. $N = 11$, 5, and 10 for plants of *A. serrulata* growing under high light in Delmarva, Georgia, and Oklahoma, respectively. $N = 19$, 5, and 10 for plants of *A. serrulata* growing under low light in Delmarva, Georgia, and Oklahoma, respectively.

[a] Percentage of open sky, calculated from mean densiometer readings taken on the north, south, east, and west sides of each specimen.

[b] Micrograms of chlorophyll per gram of dried leaf tissue.

[c] Results for high light were from plants growing under ≥50% open sky. Results for low light were from plants growing under <50% open sky.

greater survival in deep shade than did those of *A. maritima* (table 3). Seedling survival did not differ for *A. serrulata* across the three light-level treatments, but survival declined for *A. maritima* in both shade treatments. The shoots of *A. maritima* that survived were taller than those of *A. serrulata* in all three treatments, but while the shoots of *A. serrulata* showed no change in height across treatments, shoot height of *A. maritima* increased in moderate shade and decreased in deep shade (table 3). In each light-level treatment, seedlings of *A. maritima* developed greater internode length than did those of *A. serrulata* (table 3). Neither species showed an increase in internode length for seedlings in moderate shade, but internode length increased for both species under deep shade, and the increase was greater for *A. maritima* than for *A. serrulata*. In full PAR, *A. maritima* produced the greatest plant dry mass, but dry mass decreased for both species under both shade treatments (table 3). Although there were no differences in the dry mass of the two species in the two shade treatments, seedlings of *A. maritima* showed a greater decrease in dry mass in shade than did *A. serrulata*. The leaf mass ratio was greater for *A. serrulata* in both full-PAR and deep-shade treatments (table 3). Both species increased the proportion of leaf dry mass in relation to total-plant dry mass in response to moderate shade, but in deep shade the ratio decreased for *A. maritima* and continued to increase for *A. serrulata*.

Effects of Shade Stress on Photosynthesis, Growth, and Carbon Allocation

Of the four species we evaluated, *Robinia pseudoacacia* (shade-intolerant control) had the greatest concentration of chlorophyll per milligram of leaf in both sun and shade, and *A. serrulata* had the least chlorophyll in shade (table 4). While all four species showed an increase in chlorophyll in response to shade, the increase was greatest for *Cercis canadensis* (shade-tolerant control) and least for *A. serrulata*. Of plants that received the sun treatment, *A. maritima* had a higher rate of net photosynthesis than all the species except *R. pseudoacacia*, and *A. serrulata* had the lowest rate (table 4). *Alnus maritima* and *R. pseudoacacia* also had the greatest reduction in photosynthesis in response to shade, while *A. serrulata* had the least reduction. *Alnus maritima* and

Table 3

Survival, Growth, and Dry-Mass Partitioning of Young Seedlings Grown under Full PAR, Moderate Shade (Shade Fabric, 80% Reduction), or Deep Shade (Indirect PAR Only, 98% Reduction)

Dependent variable, treatment[a]	*Alnus maritima*	*Alnus serrulata*
Survival (%):		
Full PAR	97^{A}	83^{AB}
Moderate shade	73^{BC} (−25)	80^{AB}
Deep shade	57^{C} (nd,[b] −41)	80^{AB}
Shoot height (cm):		
Full PAR	4.3^{B}	2.8^{D}
Moderate shade	4.9^{A} (14)	2.7^{D}
Deep shade	3.4^{C} (−31, −21)	2.4^{D}
Internode length (cm):		
Full PAR	1.2^{BC}	0.9^{D}
Moderate shade	1.4^{B}	1.1^{CD}
Deep shade	2.3^{A} (64, 92)	1.4^{B} (27, 56)
Plant dry mass (mg):		
Full PAR	38.1^{A}	25.3^{B}
Moderate shade	13.2^{C} (−65)	12.1^{C} (−52)
Deep shade	2.3^{D} (−83, −94)	4.6^{D} (−61, −82)
Leaf mass ratio:[c]		
Full PAR	0.27^{D}	0.31^{C}
Moderate shade	0.34^{BC} (26)	0.35^{AB} (13)
Deep shade	0.21^{E} (−38, −22)	0.38^{A} (nd, 22)

Note. Means for a dependent variable marked by the same letter are not significantly different at $P \leq 0.05$, according to Fisher's least significant difference test (i.e., means separations are full factorials, and results for each variable were compared statistically both across species and across treatments). $N = 30$ for both species for the survival variable. For the other dependent variables, $N = 29$, 22, and 17 for *A. maritima* in full PAR, moderate shade, and deep shade, respectively. $N = 25$, 24, and 24 for *A. serrulata* in full PAR, moderate shade, and deep shade, respectively. Numbers in parentheses for moderate shade are the percentage change from the full-PAR treatment, and the numbers in parentheses for deep shade are, first, the percentage change from moderate shade to deep shade and, second, the percentage change from full PAR to deep shade. Percentage change is included only where means differ at $P \leq 0.05$.

[a] Mean PARs between 1000 and 1400 hours for the full-PAR, moderate-shade, and deep-shade treatments were 473, 95, and 9 μmol m^{-2} s^{-1}, respectively.

[b] nd = no significant difference (i.e., change was not determined).

[c] Ratio of leaf dry mass to whole plant dry mass.

Table 4

Chlorophyll and Photosynthetic Characteristics of Plants Grown under Full Sun or Shade (Indirect PAR Only, 96% Reduction)

Dependent variable, treatment	*Alnus maritima*	*Alnus serrulata*	*Cercis canadensis*	*Robinia pseudoacacia*
Chlorophyll[a] (mg mg^{-1}):				
Sun	0.059^{F}	0.055^{F}	0.055^{F}	0.077^{E}
Shade	0.122^{C}	0.102^{D}	0.161^{B}	0.179^{A}
Change (%)	107	85	192	132
Photosynthetic rate[b] (μmol CO_2 m^{-2} s^{-1}):				
Sun	17.1^{A}	10.2^{C}	14.6^{B}	16.1^{AB}
Shade	2.0^{D}	2.5^{D}	2.8^{D}	2.3^{D}
Change (%)	−88	−75	−81	−86
Photosynthesis per gram of chlorophyll (μmol CO_2 g^{-1} s^{-1}):				
Sun	2.26^{A}	2.09^{B}	2.11^{B}	2.33^{A}
Shade	0.28^{D}	0.51^{C}	0.25^{D}	0.30^{D}
Change (%)	−88	−76	−88	−87
Photosynthesis per gram of leaf (μmol CO_2 g^{-1} s^{-1}):				
Sun	0.132^{B}	0.113^{C}	0.113^{C}	0.180^{A}
Shade	0.034^{E}	0.051^{D}	0.040^{DE}	0.052^{D}
Change (%)	−74	−55	−65	−71
Dark respiration (μmol CO_2 g^{-1} s^{-1}):				
Sun	1.59^{B}	0.74^{C}	2.81^{A}	1.50^{B}
Shade	0.69^{C}	0.16^{D}	1.44^{B}	0.73^{C}
Change (%)	−56	−78	−49	−51
PAR compensation point[c] (μmol m^{-2} s^{-1}):				
Sun	39.4^{C}	36.9^{C}	64.8^{A}	51.6^{B}
Shade	8.7^{E}	7.9^{E}	7.9^{E}	13.8^{D}
Change (%)	−78	−79	−88	−73
Photosynthetic efficiency:[d]				
Sun	0.0310^{A}	0.0177^{BC}	0.0321^{A}	0.0310^{A}
Shade	0.0167^{C}	0.0110^{C}	0.0250^{AB}	0.0176^{BC}
Change (%)	−46	nd	nd	−43

Note. Treatment means, means separation indicators, and percentage change from sun to shade are provided for each species. Percentage change is included only where means differ at $P \leq 0.05$. Means for a dependent variable marked by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's least significant difference test. (i.e., means separations are full factorials and results for each variable were compared statistically both across species and across treatments). For the first four variables above, $N = 30$ and 10 for *A. maritima* and each of the other three species, respectively, for each species by treatment factorial classification. For the last three variables above, $N = 12$ and 4 for *A. maritima* and each of the other three species, respectively, for each species by treatment factorial classification. nd = no significant difference (i.e., change was not determined).

[a] Chlorophyll per milligram of leaf tissue.

[b] Net photosynthesis at the mean PAR between 1000 and 1400 hours, 1575 and 65 μmol m^{-2} s^{-1} for sun and shade treatments, respectively.

[c] The PAR level at which the photosynthetic rate matched the rate of plant respiration (net photosynthesis = 0 μmol CO_2 m^{-2} s^{-1}).

[d] Increase in net photosynthesis per unit PAR from 0 to 400 μmol m^{-2} s^{-1} and calculated as the slope of the linear regression for photosynthesis at PAR of 0, 200, and 400 μmol m^{-2} s^{-1}. $N = 12$ for *A. maritima* and $N = 4$ for each of the other three species.

R. pseudoacacia in the sun had the highest rate of photosynthesis per gram of chlorophyll. In shade, *A. serrulata* had the least reduction in photosynthesis per gram of chlorophyll and the greatest photosynthesis per gram of chlorophyll. *Robinia pseudoacacia* had the greatest photosynthesis per gram of leaf tissue in the sun, while *A. serrulata* and *C. canadensis* had the lowest. *Alnus maritima* and *R. pseudoacacia* showed the greatest reduction in photosynthesis per gram of leaf tissue in response to shade, while *A. serrulata* showed the least reduction. *Alnus maritima* had the lowest rate of photosynthesis per gram of leaf tissue in the shade. Dark respiration rate decreased for all four species in response to shade, and *A. serrulata* had the lowest respiration rate under both treatments and the greatest percentage reduction in respiration in response to shade. Respiration rate was similar for *A. maritima* and *R. pseudoacacia* in both treatments, and shade-tolerant *C. canadensis* had the greatest respiration rate in both the sun and shade treatments. The two *Alnus* species had the lowest

PAR compensation points in the sun, while *C. canadensis* had the highest (table 4). *Cercis canadensis* and *R. pseudoacacia* had the greatest and least reduction in compensation point, respectively, and *R. pseudoacacia* had the highest compensation point in the shade. PAR compensation point was similar for the two *Alnus* species and *C. canadensis* in the shade. The photosynthetic efficiency of *A. serrulata* was 43% lower than that of the other three species in the sun, but *A. serrulata* and *C. canadensis* showed no reduction in photosynthetic efficiency in response to shade, while the efficiency of the other two species decreased by more than 40% (table 4).

Robinia pseudoacacia and *A. maritima* attained the greatest and second-greatest shoot dry masses in the sun over the 4-mo experiment, but while these two species showed more than 80% reduction in response to shade, the shoot dry masses of *A. serrulata* and *C. canadensis* were not reduced by shade (table 5). All values of canopy shape (the ratio of canopy height to canopy diameter) were greater than 1, revealing that the canopy height was greater than the canopy width for all species in both treatments, but only *R. pseudoacacia* and *A. maritima* showed an increase in the canopy shape ratio in response to shade (table 5). The leaf : shoot dry-mass ratio was greater than 0.50 for all species except *R. pseudoacacia*, indicating that this species was the only one of the four to partition more dry mass into the stems than into the leaves. *Alnus maritima* and *A. serrulata* had the greatest leaf : shoot ratio in the sun, but the ratio decreased for *A. maritima*, increased for *R. pseudoacacia*, and was unchanged for *A. serrulata* and *C. canadensis* in response to shade. *Alnus serrulata* had the greatest leaf area density in both the sun and shade, but while there was no change for *C. canadensis*, leaf area density decreased for the two *Alnus* species in response to shade (table 5). Specific leaf mass decreased for all four species in response to shade. *Alnus maritima* and *C. canadensis* had the greatest specific leaf mass in the sun and the greatest reduction in response to shade, although *A. serrulata* showed the lowest specific leaf mass in the shade.

Discussion

Shade Tolerance

Thorough analyses of shade tolerance should account for the numerous mechanisms and adjustments in growth, carbon allocation, and physiology that interact to determine resistance to shade stress (Daubenmire 1962; Levitt 1980; Kozlowski et al. 1991). Seedlings of shade-tolerant species often grow more slowly than those of shade-intolerant species in high light but are able to maintain adequate rates of growth in low light (Kobe et al. 1995; Veneklaas and Poorter 1998; Walters and Reich 1999). Our examination of *Alnus*

Table 5

Growth, Dry Mass Partitioning, and Morphometrics of Plants Grown under Full Sun or Shade (Indirect PAR Only, 96% Reduction)

Dependent variable, treatment	*Alnus maritima*	*Alnus serrulata*	*Cercis canadensis*	*Robinia pseudoacacia*
Shoot dry mass (g):				
Sun	28.0^{B}	4.8^{DE}	20.1^{C}	285.0^{A}
Shade	5.1^{DE}	2.0^{E}	10.4^{CD}	49.0^{B}
Change (%)	−82	nd	nd	−83
Canopy shape:[a]				
Sun	1.58^{C}	1.45^{C}	3.25^{A}	2.17^{B}
Shade	2.03^{B}	1.54^{C}	3.07^{A}	3.32^{A}
Change (%)	28	nd	nd	53
Leaf : shoot ratio (g g^{-1}):				
Sun	0.59^{A}	0.60^{A}	0.51^{CD}	0.34^{F}
Shade	0.52^{C}	0.56^{AB}	0.53^{BC}	0.49^{D}
Change (%)	−12	nd	nd	44
Leaf area density[b] (mm^2 cm^{-3}):				
Sun	5.3^{C}	10.0^{A}	3.1^{E}	
Shade	4.1^{D}	7.5^{B}	2.7^{E}	
Change (%)	−23	−25	nd	
Specific leaf mass (mg cm^{-2}):				
Sun	13.0^{A}	9.1^{B}	12.9^{A}	9.6^{B}
Shade	5.9^{C}	4.9^{D}	5.8^{C}	7.3^{C}
Change (%)	−55	−46	−55	−24

Note. Treatment means, means separation indicators, and percentage change from sun to shade are provided for each species. Percentage change is included only where means differ at $P \leq 0.05$. Means for a dependent variable marked by the same letter are not significantly different at $P \leq 0.05$ according to Fisher's least significant difference test. (i.e., means separations are full factorials and results for each variable were compared statistically both across species and across treatments). $N = 60$ for *A. maritima*, and $N = 20$ for each of the other three species for each species × treatment factorial classification. nd = no significant difference (i.e., change was not determined).

[a] Canopy shape = shoot height/canopy diameter.

[b] Leaf area density = plant leaf area/canopy volume. Leaf area of *R. pseudoacacia* was not measured.

maritima and *Alnus serrulata* revealed that seedlings of *A. serrulata* accumulated less dry mass in high light than did those of *A. maritima* over the duration of our experiments (tables 3, 5), but while the dry mass of *A. maritima* decreased sharply in response to shade, the dry mass of *A. serrulata* either did not decrease (table 5) or decreased less than that of *A. maritima* (table 3). Along with differences in growth rate, plants also adjust carbon allocation to increase efficiency of trapping PAR (i.e., show plasticity), and the most efficient species accomplish this with a minimum expenditure of resources (Levitt 1980). Therefore, shade-tolerant species that employ this mechanism partition a greater percentage of their biomass to leaves, as opposed to nonphotosynthetic tissues (i.e., high leaf area or leaf mass to plant mass ratio) and develop leaves of lower specific mass (Loach 1970; Givnish 1988; Callaway 1992; Poorter et al. 1995; Knapp and Carter 1998). Differences in carbon allocation between the two *Alnus* species suggest greater shade tolerance or plasticity for *A. serrulata* than for *A. maritima*. Young seedlings of *A. serrulata* developed a greater leaf mass ratio in the shade than did seedlings of *A. maritima* (table 3), and while *A. serrulata* demonstrated plasticity by increasing leaf mass ratio in both shade treatments, *A. maritima* increased leaf mass ratio in moderate shade and decreased this ratio in deep shade, indicating stress in deep shade. Results were similar for older seedlings, where the leaf : shoot ratio was greater for *A. serrulata* than for *A. maritima* in the shade (table 5), and the ratio again decreased for *A. maritima* in response to shade. Older seedlings of *A. serrulata* developed leaves of lower specific mass than did those of *A. maritima* in both sun and shade (table 5), a characteristic of efficient energy investment that was also found in mature naturally occurring *A. serrulata* growing in low light (table 2).

Leaves of shade-tolerant species generally have a higher content of chlorophyll by mass and a lower chlorophyll *a* : *b* ratio than do leaves of intolerant species (Goodchild et al. 1972; Boardman 1977; Lichenthaler et al. 1981; Kozlowski et al. 1991). Our assessment of mature plants in native habitats showed greater chlorophyll content for *A. serrulata* in low light than for *A. maritima* and a lower chlorophyll *a* : *b* ratio for *A. serrulata* in both light levels in all provenances except Georgia (table 2). Unlike the mature plants, leaves of *A. serrulata* seedlings had less chlorophyll by mass in the shade than leaves of *A. maritima*, *Cercis canadensis*, or our shade-intolerant control, *Robinia pseudoacacia* (table 4). Although these results seem to contradict those for mature plants and seem to indicate lower shade tolerance for *A. serrulata*, our results for photosynthesis per gram of chlorophyll and photosynthesis per gram of leaf resolve these conflicts. Although *A. serrulata* had the lowest chlorophyll content in the shade, it had the highest photosynthesis per gram of chlorophyll and higher photosynthesis per gram of leaf in the shade than did *A. maritima* (table 4), again suggesting greater efficiency per energy invested by seedlings of *A. serrulata*.

Of the two control species in our experiment with 3-mo-old seedlings, the light responses of *A. maritima* more closely resembled those of shade-intolerant *R. pseudoacacia* than those of *C. canadensis*. *Alnus maritima* and *R. pseudoacacia* had the greatest accumulations of shoot dry mass in the sun and similar percentages of decrease in dry mass in response to shade (table 5). They had the greatest net photosynthesis in sun, the greatest reduction due to shade, the greatest photosynthesis per gram of chlorophyll in sun, and the greatest decrease in photosynthesis per gram of leaf due to shade and were the only two species to have lower photosynthetic efficiency (Loach 1967; Bazzaz 1979) in the sun than in the shade (table 4), all characteristics consistent with shade intolerance. The light responses of *A. serrulata* most closely resembled those of our shade-tolerant control, *C. canadensis*. *Alnus serrulata* and *C. canadensis* showed no decrease in shoot dry mass and no change in canopy shape or leaf : shoot ratio in response to shade (table 5). They had identical leaf chlorophyll contents and photosynthesis per gram of leaf in sun, identical PAR compensation points in shade, and no reduction in photosynthetic efficiency in response to shade (table 4).

Two of the most important indicators of shade tolerance of woody species are seedling survivorship under shade (Kobe et al. 1995; Delagrange et al. 2004) and the light characteristics under which plants are found in nature (Bazzaz 1979; Hicks and Chabot 1985). Young seedlings of *A. serrulata* showed the same percentage of survival in deep shade as they did in full sun, but the survival of *A. maritima* decreased by 25% in moderate shade and 41% in deep shade (table 3). In the three natural provenances, mature *A. serrulata* was found growing in shadier locations (lower percentage open sky) than was mature *A. maritima* (table 2). We conclude that *A. maritima* should be classified as very intolerant of shade on an ecological basis, which includes natural survival of young seedlings, and classified as intolerant when considering its potential application in managed landscapes that would not include natural regeneration. *Alnus serrulata* should be classified as tolerant of shade on both an ecological and a horticultural basis.

Mechanisms

One of the key physiological characteristics of shade-tolerant species is the low rate of respiration that enables them to maintain plant health and metabolism at low light levels (Loach 1967; Boardman 1977; Bazzaz 1979). Although seedlings of *A. serrulata* had the least chlorophyll of any of the species in the shade, they also had the lowest rate of dark respiration in both sun and shade and the greatest percentage reduction in respiration in response to shade (table 4). This illustrates two features of *A. serrulata*: (1) plants were not under stress in the shade, and (2) an important mechanism in the shade tolerance of *A. serrulata* is its very low and highly adaptable dark respiration rate (table 4), which allows it to maintain adequate whole-plant carbon balance at low light levels (Levitt 1980; Kozlowski et al. 1991). Our results suggest that, although they both are shade-tolerant species and both have a low PAR compensation point in the shade, the physiological mechanisms employed by *A. serrulata* and *C. canadensis* are different. While *A. serrulata* achieves its resistance to shade stress mainly through a reduction in respiration, *C. canadensis* maintains a much higher respiration rate and compensates through a large increase in leaf chlorophyll concentration, very high photosynthetic efficiency (table 4), and, presumably, a very high gross rate of photosynthesis in shade.

Although *A. maritima* did demonstrate plasticity in its rate of respiration, its response was much like that of shade-intolerant *R. pseudoacacia* and does not appear to be an

important mechanism in its resistance to shade stress (table 4). Its very low photosynthesis per gram of leaf illustrates that *A. maritima* continued to invest large amounts of energy in the development of leaves that were inefficient in the shade. The carbon allocation responses of *A. maritima* and *R. pseudoacacia* revealed typical "shade avoidance" mechanisms often employed by intolerant species (Ballaré et al. 1997; Schmitt 1997; Henry and Aarssen 2001). While shoot elongation (canopy shape) increased for these two species in response to shade, there were no increases for the two shade-tolerant species (table 5). The decrease in the leaf : shoot ratio of seedlings of *A. maritima* in shade suggests a response that partitioned a disproportionate amount of carbon resources to stem size at the expense of photosynthetic tissues that were essential in conditions of unavoidable shade. Shoot height of young seedlings of *A. maritima* increased in moderate shade, but there was no change for *A. serrulata*, and internode length increased more for *A. maritima* than it did for *A. serrulata* in response to deep shade (table 3). The low survival rate of *A. maritima* demonstrates that while seedlings elongated to avoid shade, they were less able to cope when shade stress was unavoidable.

Ecology

Alnus maritima and *A. serrulata* are similar in many ways. They are both large, multitrunked shrubs that prefer wet soils. They are sympatric in Georgia and on the Delmarva Peninsula and are both found only in eastern North America. They both fix nitrogen in symbiotic relationship with *Frankia* bacteria, a strong indicator that they might function well as pioneer shrubs in both primary (Richardson and Evans 1986; Morris and Wood 1989; del Moral and Wood 1993) and secondary forest succession (Tarrant and Trappe 1971; Uemura 1971; Binkley 1992) by augmenting the available resources to a level required by later-successional species (Ugolini 1968; Connell and Slatyer 1977; Chapin et al. 1994). But unlike *A. maritima*, which closely resembles the general profile of an early-successional shrub (i.e., shade intolerance, fast growth in full sun, short life span, broad fundamental niche; Odum 1969; Connell and Slatyer 1977; Bazzaz 1979; Kozlowski et al. 1991; Lawesson and Oksanen 2002), *A. serrulata* is tolerant of shade. As both species can and do function as early-successional species with relatively short life spans (Furlow 1979), they die and are replaced more frequently than longer-lived late-succession species (Connell and Slatyer 1977). With its high seedling mortality in shade (table 3), *A. maritima* is much less likely than *A. serrulata* to be replaced by its own propagules in the presence of adults of its own or other species. While naturally occurring colonies of *A. maritima* are found only in wet areas with abundant sunlight, colonies of *A. serrulata* are often found growing along waterways as part of the forest understory. This capacity of *A. serrulata* to persist as a shade-tolerant member of the understory is a major factor contributing to the greater ecological success of this species over that of *A. maritima*.

While *A. maritima* has a broad fundamental niche, its realized niche appears to be rather narrow. *Alnus maritima* is most competitive in locations with abundant sunlight and very wet, nutrient-poor soil conditions that can be harmful to or insufficient for most other woody species (Schrader and Graves 2002; Schrader et al. 2005). The capacity of *A. maritima* to thrive in severe environments would make it extremely well suited for primary forest succession (Ugolini 1968; Chapin et al. 1994) but less competitive during secondary succession, when soil nutrients or soil moisture are less prohibitive of other species (Connell and Slatyer 1977). The present rarity of *A. maritima* might best be explained by its specialized and narrow realized niche and by the absence of opportunities to serve its role in primary forest succession within its range over the last 10,000 yr. During the late Pleistocene Epoch, successive episodes of glacial progression and recession and numerous episodes of widespread sediment deposition and subsequent erosion, especially in the Mississippi River drainage basin (Esling and Halberg 1985; Hajic 1985; Lively and Alexander 1985), would have provided extensive and continuous opportunities for colonization of *A. maritima* on wet, disturbed sites in full sunlight (Shelford 1954; Ugolini 1968; Bedinger 1978; Chapin et al. 1994). With the retreat of the last great glacier (the Wisconsin ice sheet), the resumption of drainage of the Great Lakes via the St. Lawrence River, and the opening of the outlet channel for Glacial Lake Agassiz to the northeast about 10,000 yr ago, the Mississippi River basin and many other watersheds of central and eastern North America have experienced a long period of relative stability (Delcourt and Delcourt 1993; Saucier 1994). This stability has allowed most of the floodplain forests of the Mississippi River basin to remain at transitional or mature succession for thousands of years (Wiener et al. 1998; Fremling and Drazkowski 2000), and the scarcity of opportunities for *A. maritima* to facilitate in primary succession over this time is a likely cause for its extremely limited distribution. *Alnus serrulata* is capable of serving a pioneer role similar to that of *A. maritima* (Furlow 1979) but would be less competitive than *A. maritima* in primary succession. Its shade tolerance would make *A. serrulata* more competitive than *A. maritima* in later successional stages.

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